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How Dispersal Limitation Shapes Species–Body Size Distributions in Local Communities

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ABSTRACT: A critical but poorly understood pattern in macroecology is the often unimodal species–body size distribution (also known as body size–diversity relationship) in a local community (embedded in a much larger regional species pool). Purely neutral community models that assume functional equivalence among species are incapable of explaining this pattern because body size is the key determinant of functional differences between species. Several niche-based explanations have been offered, but none of them is completely satisfactory. Here we develop a simple model that unites a neutral community model with niche-based theory to explain the relationship. In the model, species of similar size are assumed to belong to the same size guild. Within a size guild, all individuals are equivalent in their competition for resources, *sensu* Hubbell's neutral community model; they have the same speciation rate and dispersal capacities. Between size guilds, however, the total number of individuals, the speciation rate, and the dispersal capacities differ, but using known allometric scaling laws for these properties, we can describe the differences between size guilds. Our model predicts that species richness reaches an optimum at an intermediate body size, in agreement with observations. The optimum at intermediate body size is basically the result of a trade-off between, on the one hand, allometric scaling laws for the number of individuals and the speciation rate that decrease with body size and, on the other hand, the scaling law for active dispersal that increases with body size.

Keywords: macroecology, biodiversity, community, niche-based model, neutral model, allometric scaling law.

Biodiversity is currently decreasing at an unprecedented rate. Counteracting this trend requires a thorough understanding of biodiversity in ecological communities. To this

end, studying large-scale biodiversity patterns that link species richness to variation in species traits within and across ecological communities has proved to be useful (May 1986; Brown and Maurer 1989; Brown 1995; Lawton 1999; Maurer 1999; Gaston and Blackburn 2000; Hubbell 2001). The most prominent examples of such patterns are the species–area curve, the distribution of relative abundances, and the species–body size distribution. In this article, we focus on the species–body size distribution (also known as the body size–diversity relationship) that is typically presented as a histogram of the number of species in several logarithmic body size classes.

The general form of this pattern has been subject to debate. A confusing factor is that the phylogenetic pattern (e.g., of all mammals or birds) is often reported (Blackburn and Gaston 1998; Gittleman and Purvis 1998; Gardezi and da Silva 1999; Owens et al. 1999; Orme et al. 2002), whereas we focus here on the pattern in a local community because we are interested in the ecological processes underlying it. Most of the studies report a unimodal, right-skewed shape for the species–body size distribution in a community (Dial and Marzluff 1988; Blackburn and Gaston 1994; Brown 1995; Dixon et al. 1995; Siemann et al. 1996, 1999; Gregory 1998; Osler and Beattie 1999; Bakker and Kelt 2000; Gaston and Blackburn 2000; Gomez and Espadaler 2000). Nevertheless, the optimum at intermediate body size is not always very pronounced, there is much variation in skewness, and bimodal shapes are also observed (Chown and Gaston 1997; Bakker and Kelt 2000; Gaston and Blackburn 2000; Gaston et al. 2001). Early studies even suggested that the classes of the smallest body sizes are the most speciose, and they explained the observed optimum at intermediate body size by poor sampling of small species (Van Valen 1973; May 1978, 1986; see, however, Hutchinson and MacArthur 1959). Yet, nowadays consensus has grown that the diversity peak at intermediate body size is real.

Four types of explanations of the unimodality of the species–body size pattern have been proposed (reviewed by Gaston and Blackburn 2000). However, we argue that none of them is completely satisfactory. First, several au-

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thors suggest that size differences explain niche partitioning in space. Hutchinson and MacArthur (1959) view the landscape as consisting of equally sized mosaic elements of different types, assume that larger organisms require a larger number of elements, and show that the number of niches defined as the number of distinct combinations of types first sharply increases with body size and then drops slowly. This model is attractive for its simplicity, but it cannot, among other things, accommodate spatial turnover in species identities (Gaston and Blackburn 2000). Its underlying idea has been connected to the fractal nature of the environment that provides more niches for smaller species because they perceive more detail (Morse et al. 1985); however, the optimum at intermediate body size is lost in these fractal explanations. An exception is the article by Ritchie and Olff (1999), but they find a left-skewed distribution and are hesitant about the application of their model to communities with species that use different resources or habitat. Second, the species–body size pattern for a certain trophic level may reflect the species–body size pattern of the next lower trophic level (Warren and Lawton 1987; Dixon et al. 1995). Obviously, this type of explanation is not an ultimate explanation (but see the discussion). Third, Brown et al. (1993) predict the existence of an optimal body size using an energetic model of fitness with a trade-off between energy uptake and energy conversion into offspring. Brown (1995) then envisages that evolution will result in a unimodal body size distribution in an ecological community because once species with the optimal body size have occupied their niche, the optimal body size is no longer “available” in a community, so other species have to resort to body sizes close to the optimum. Although interesting, this idea has not been worked out sufficiently to allow quantitative predictions of species–body size distributions. Fourth, Koziowski and Weiner (1997), backed up by Kindlmann et al. (1999), predict an optimal body size based on a trade-off between production and mortality, and they show that for different, lognormally distributed model parameters, the distribution of optimal body sizes is right-skewed in most cases. Again, a more than verbal argument is lacking of how such a distribution will yield the unimodal pattern observed in an ecological community.

All these explanations can be classified as niche-based explanations. Niche-based theories of biodiversity treat different species as functionally different; each species has unique functional characteristics that allow it to capture sufficient resources to be able to persist. Coexistence of species is possible if resources are sufficiently diverse, that is, if there is a sufficient number of limiting factors (MacArthur 1970; Schoener 1974; Tilman 1982; Mouquet and Loreau 2002). In contrast, neutral theories emphasize the functional equivalence of species: all species behave alike

in community processes, for example, in competition for resources and dispersal (MacArthur and Wilson 1967; Chesson and Warner 1981; Fagerström 1988; Bramson et al. 1996; Bell 2000, 2001; Hubbell 2001). Neutral processes eventually lead to stochastic extinction of species until only one species is present (monodominance), but coexistence is possible if species extinction is counteracted by speciation in or immigration into the community. And even in the case where speciation and immigration are considered negligible, species can be said to coexist in practice because the time to monodominance can be extremely long (Hubbell 2001). Neutral theories by themselves cannot explain the observed species–body size distribution because body size is the key determinant of functional differences between species (Peters 1983) and is therefore alien to any theory formulated purely from a neutral perspective. However, a theory combining both niche-based and neutral elements may be able to explain the species–body size distribution. It is such a hybrid explanation that we present in this article.

Our critical proposition is that neutral theory holds among species with small differences in body size, making them functionally equivalent, while niche-based allometric scaling laws hold for species groups of different sizes. Allometric relationships between resource or energy use and body size in fact ultimately constitute the basis of all of the aforementioned attempts to explain the species–body size pattern. Although allometric relationships have thus far been mainly applied to predict metabolism and growth (Gillooly et al. 2001, 2002; West et al. 2001, 2002), they are equally well applicable to movement, as realized by Peters (1983), and hence to dispersal. With dispersal being an essential ingredient of neutral models (but certainly also important in niche-based models; see, e.g., Levin 1974; Hastings 1980; Holt 1993; Tilman 1994; Mouquet and Loreau 2002), allometric scaling laws of dispersal provide a link between niche-based and neutral elements. We will demonstrate that such a scaling law is crucial in our explanation.

Model

Combining Neutral and Adaptive Processes: A Community Composed of Body Size Guilds

As proposed above, we envision that a local community is composed of several groups of species of similar size. We will refer to these groups as body size guilds. Guild k contains all species with body mass between M_k/r_k and $r_k M_k$, where $r_k > 1$. Because we assume that each guild corresponds to a niche and that niches are adjacent without overlap (which is reasonable if size differences $[r_k]$ are sufficiently large; Prins and Olff 1998), the size guilds are

also adjacent without overlap. Hence, guild $k + 1$ contains all species with body mass between $r_k M_k = M_{k+1}/r_{k+1}$ and $r_{k+1} M_{k+1}$. Equating body size to niche in this way is not unreasonable since species of sufficiently different sizes often utilize different resources or different parts of the size spectrum or availability spectrum of a single resource.

Within each guild, Hubbell's (2001) neutral model is assumed to apply, whereas the differences between guilds are captured by allometric scaling laws. Our explanation of the unimodal species–body size distribution therefore comes down to integrating within-guild and between-guild resource partitioning.

For simplicity, we set $r_k = r$ for all k . This means that on a logarithmic scale, all body size classes are equally wide with width $2 \log r$ (and central body size M_k). We will discuss this choice later. The parameter r gives an indication of the relative contribution of the niche-based and neutral model elements to community structure. If r is large, species of widely different body sizes are assumed to be functionally equivalent, and stochasticity mostly determines biodiversity. If r is small, each guild contains only a few species, and niches are the dominant determinants of biodiversity. This does not mean that neutral processes no longer occur; they still operate within a size guild.

In the first part of the model description, we will show how species richness within a guild is determined by a modified formulation of Hubbell's neutral model. The species–body size distribution is just a histogram (with logarithmic body size classes) of the number of species in each guild. To obtain it, we need to know how the parameters in Hubbell's model that determine species richness in each guild depend on body size. In the second part of the model description, we will therefore establish relationships between these parameters and body size using allometric scaling laws to predict diversity over multiple body size guilds.

Within-Guild Processes: Hubbell's Neutral Model

In Hubbell's (2001) unified neutral model of biodiversity and biogeography, functionally similar species form a metacommunity where species extinction is balanced by speciation. In the local community, species extinction is balanced by immigration from the metacommunity. Hubbell's metacommunity concept is in fact not much more than a reservoir of all individuals of all species that occur in a region. We prefer to use the term “regional species pool” for this and reserve the term “metacommunity” for a network of local communities linked by dispersal similar to the definition of a metapopulation as a network of local populations linked by dispersal. Individuals of all species are assumed to have equal mortality, immigration, and speciation rates; this is the neutrality assumption. They

play a zero-sum (i.e., the total number of individuals remains constant) game in which each site becoming vacant because of the death of an individual is immediately occupied by offspring of a member of the local community or by an immigrant, in proportion to the frequency of the species in the local community or regional species pool, respectively. If there is no immigration, that is, species dispersal is extremely limited, the local community will eventually contain only a single species (monodominance). If there is some immigration, coexistence of species is the result of a balance between species extinction and immigration; the number of coexisting species depends on the degree of dispersal limitation. If there is no dispersal limitation, the distribution of species in the local community is equal to that in the regional species pool.

In a local community with J individuals without dispersal limitation, the expected number of species is given by (Hubbell 2001)

$$S(\theta, J) = \theta \sum_{i=1}^J \frac{1}{\theta + i - 1}, \quad (1)$$

where

$$\theta = 2J_M \nu. \quad (2)$$

Here J_M is the number of individuals in the regional species pool and ν is the speciation rate. Although these quantities may be hard to measure (Abrams 2001), they do have a simple and biologically meaningful interpretation, and so the somewhat obscure composite parameter θ is also biologically meaningful.

Equation (1) can be easily understood, since the quantity $\theta/(\theta + i - 1)$ is the probability that the i th individual is of a new species, that is, a species not yet encountered in the $i - 1$ previous individuals. Summing the probabilities for all i gives the expected number of species. This number increases with θ (and thus with J_M and ν) and with J .

Equation (1) assumes the absence of dispersal limitation: a vacant site in the local community is always colonized by a species from outside the local community; hence, the probability of immigration into the local community (m) is equal to unity. For dispersal-limited species ($m < 1$), Hubbell proposes the following formula,

$$S(\theta, J) = \theta \sum_{i=1}^J \frac{m(i)}{\theta + i - 1}, \quad (3)$$

with a phenomenological function for $m(i)$,

$$m(i) = i^{-\omega}, \quad (4)$$

where ω is some indicator of the degree of dispersal limitation (which is the same for all species). This formulation of dispersal limitation models a dilution effect: the larger the community, the more likely a vacant site is filled by a local individual than by an immigrant.

The term $\theta m(i)/(\theta + i - 1)$ should again be interpreted as the probability that the i th individual is a new species not encountered in the $i - 1$ previous individuals. This probability is the product of the probability that it is a descendent of an immigrant that has no offspring among the $i - 1$ previous individuals and the probability that the immigrant is of a new species. However, equation (3) is not consistent with this interpretation. In appendix A in the online edition of the *American Naturalist*, we derive a consistent formula that can be approximated very accurately by either of the following formulas:

$$S(\theta, J) = \theta \sum_{i=1}^J \frac{m(i)}{\theta + \sum_{j=1}^{i-1} m(j)}, \quad (5a)$$

$$S(\theta, J) = \theta \sum_{i=1}^{\sum_{j=1}^J m(j)} \frac{1}{\theta + i - 1}. \quad (5b)$$

A remaining problem is that Hubbell's proposal for $m(i)$, equation (4), has no clear connection to familiar dispersal parameters such as mean or maximum dispersal distance, because ω is an unmeasurable quantity. This calls for a simple and more mechanistic treatment of dispersal limitation. We propose the following model. Imagine that the i th site is equally available to $i - 1$ locals and I immigrants. Then, the probability $m(i)$ that the i th individual descends from an immigrant that has no offspring among the $i - 1$ locals is given by

$$m(i) = \frac{I}{I + i - 1} \quad (6)$$

(see app. B in the online edition of the *American Naturalist*).

If a site is available to each immigrant with probability $p = 1$ (no dispersal limitation), then $I = J_M - J$ and $m(i) \approx 1$ for all i because $J_M \gg J > i$. However, if the site is available with a probability $p < 1$, then I is the effective number of immigrants, $I = (J_M - J)p$ (see app. C in the online edition of the *American Naturalist*). Taking all this into account results in

$$m(i) = \frac{(J_M - J)p}{(J_M - J)p + i - 1}. \quad (7)$$

The probability p may depend on the mean dispersal distance of an immigrant, α^{-1} , as

$$p = e^{-\alpha D} \quad (8)$$

(Hanski 1994), where D is the effective distance between the regional species pool and the local community. The variable D is determined by the geographic setting of the community; large D is expected for islands or fragmented landscapes. However, the exponential decline of dispersal probability has been criticized for being too steep (Schwartz 1993; Hill et al. 1996; Clark et al. 1999). An alternative dispersal kernel having a fatter tail (higher probability of long-distance dispersal) is a power function:

$$p = \left\{ \frac{1}{1 + [1/(x - 2)]\alpha D} \right\}^x, \quad (9)$$

where x is a parameter measuring the fatness of the tail; x must be > 2 to avoid the zeroth and first-order moments to become infinite. This dispersal kernel also has mean dispersal distance α^{-1} . In fact, equation (9) becomes equation (8) in the limit for $x \rightarrow \infty$.

In sum, the full within-guild model is specified by equations (5), (7), and (8) or (9) and contains four or five species/community-specific parameters (J_M , ν , J , α , and possibly x) and one parameter that is defined by the geographic setting of the community (D). See also table 1, where the full model is summarized.

Between-Guild Processes: Allometric Scaling Laws

As we explained above, to obtain the species–body size distribution, we now need to know how the expected number of species in the community depends on the central body size M_k of guild k . Because species richness is fully determined by the model parameters J_M , ν , J , α (and x if eq. [9] is used), and D , we need to know how these parameters depend on body size M_k . In other words, we need to establish allometric scaling laws for these parameters. We first note that D is independent of body size because it is a geographical property of the community. Furthermore, we assume that the shape parameter x of equation (9) does not depend on body size. Let us then assume that for a certain guild with central body size M_0 , the remaining aforementioned parameters are $J_{M,0}$, ν_0 , J_0 , and α_0 . Allometric scaling laws then can be used to determine the values of the parameter for guilds with different central body size M_k .

The Number of Individuals in the Local Community and Regional Species Pool J_k and $J_{M,k}$. Denote the total amount of resources available to guild k by R_k and the per capita resource use of individuals in guild k by \hat{R}_k . Because we

Table 1: Full model used to explain the observed unimodal species–body size distribution

| Symbol | Definition | Default value (used in figs. 1–5) |
|--|--|--------------------------------------|
| Variables: | | |
| S_k | Number of species in guild k | |
| θ_k | Hubbell’s fundamental biodiversity number in guild k (reflects diversity in the regional species pool) | |
| $m_k(i)$ | Probability that the i th individual in guild k has no local ancestors in common with the previous $i - 1$ individuals | |
| p_k | Probability that an immigrant in guild k will disperse a distance D | |
| M_k | Body size of species in guild k | |
| J_k | Number of individuals in guild k in local community | |
| $J_{M,k}$ | Number of individuals in guild k in regional species pool | |
| ν_k | Speciation rate of species in guild k | |
| α_k^{-1} | Mean dispersal distance of species in guild k | |
| Parameters: | | |
| M_0 | Body size of species in reference guild (= guild 0) | 1 |
| J_0 | Number of individuals in reference guild in local community | 10^3 |
| $J_{M,0}$ | Number of individuals in reference guild in regional spe- cies pool | 10^9 |
| ν_0 | Speciation rate of species in reference guild | 10^{-10} |
| α_0^{-1} | Mean dispersal distance of species in reference guild | .5 |
| x | Parameter determining the shape of the dispersal kernel | 5 |
| D | System parameter defining the effective distance between the local community and the regional species pool | 1 |
| b | Allometric scaling parameter in scaling law of J and J_M | $-3/4$ |
| c | Allometric scaling parameter in scaling law of ν | $-1/4$ |
| d | Allometric scaling parameter in scaling law of α^{-1} | .65 |
| Formulas: | | |
| Within-guild processes: | | |
| $S_k(\theta_k, J_k) = \theta_k \sum_{i=1}^{J_k} \frac{m_k(i)}{\theta_k + \sum_{j=1}^{i-1} m_k(j)}$ | | |
| $\theta_k = 2J_{M,k}\nu_k$ | | |
| $m_k(i) = \frac{(J_{M,k} - J_k)p_k}{(J_{M,k} - J_k)p_k + i - 1}$ | | |
| $p_k = \left\{ \frac{1}{1 + [1/(x - 2)]\alpha_k D} \right\}^x$ | | |
| Between-guild processes: | | |
| $J_k = J_0 \left(\frac{M_k}{M_0} \right)^b$ | | |
| $J_{M,k} = J_{M,0} \left(\frac{M_k}{M_0} \right)^b$ | | |
| $\nu_k = \nu_0 \left(\frac{M_k}{M_0} \right)^c$ | | |
| $\alpha_k^{-1} = \alpha_0^{-1} \left(\frac{M_k}{M_0} \right)^d$ | | |

assume that individuals within a guild play a zero-sum game, all resources available to a guild will be used, so J and J_M are given by

$$J_k = \frac{R_k}{\hat{R}_k}, \quad (10)$$

$$J_{M,k} = \frac{R_{M,k}}{\hat{R}_k}. \quad (11)$$

The question is now how R_k and \hat{R}_k scale with body mass. An individual of a large species generally needs more resources than an individual of a small species; that is, the per capita resource use \hat{R}_k is larger. We can express this observation in mathematical terms as

$$\hat{R}_k = \hat{R}_0 \left(\frac{M_k}{M_0} \right)^{\hat{a}}, \quad (12)$$

where \hat{a} lies probably between 3/4 for energy- or nutrient-limited species and 1 for space-limited species (Brown 1995). The variable \hat{R}_0 is the per capita resource use in the reference guild. The scaling of R_k and $R_{M,k}$, the total amount of resources available to guild k in the local community and regional species pool, respectively, is less clear and perhaps one of the most contentious issues in macroecology (Gaston and Blackburn 2000). We propose that

$$R_k = R_0 \left(\frac{M_k}{M_0} \right)^a, \quad (13)$$

$$R_{M,k} = R_{M,0} \left(\frac{M_k}{M_0} \right)^a, \quad (14)$$

where R_0 and $R_{M,0}$ again refer to the reference guild and a determines whether large or small species have more resources available to them; $a = 0$ implies that all guilds have an equal amount of resources available to them (Damuth 1981, 1987); $a > 0$ favors large species (Brown and Maurer 1986), whereas $a < 0$ favors small species (Griffiths 1998). There are several conceivable mechanisms determining the sign and value of a , but the distribution of resources over the guilds may also depend on the community under consideration so that any value of a may obtain or even that other functional relationships than proposals (13) and (14) may apply. We will come back to proposals (13) and (14) and the value of a in the discussion. Combining equation (12) with proposals (13) and (14) leads to

$$J_k = J_0 \left(\frac{M_k}{M_0} \right)^b, \quad (15)$$

$$J_{M,k} = J_{M,0} \left(\frac{M_k}{M_0} \right)^b, \quad (16)$$

where $b = a - \hat{a}$, $J_0 = R_0/\hat{R}_0$, and $J_{M,0} = R_{M,0}/\hat{R}_0$. Direct estimates of b may be obtained from abundance–body size data, which suggest that b lies between -1 and -0.5 . We will return to this direct method in the discussion.

The Speciation Rate ν_k . Because speciation rate may scale as the inverse of biological time (e.g., developmental time, life span), which seems to scale as $M^{1/4}$ (Peters 1983; Gillooly et al. 2001, 2002), we have

$$\nu_k = \nu_0 \left(\frac{M_k}{M_0} \right)^c, \quad (17)$$

with $c = -1/4$. Dial and Marzluff (1988) also support a monotonically decreasing curve of speciation rate versus body mass.

Combining equations (17) and (16), we have the following for θ :

$$\theta_k = \theta_0 \left(\frac{M_k}{M_0} \right)^{b+c}, \quad (18)$$

with $\theta_0 = 2J_{M,0}\nu_0$.

The Inverse Dispersal Distance α_k . For our model of dispersal limitation, we need to know how α_k , the inverse dispersal distance, scales with body mass. Sutherland et al. (2000) suggest an allometric scaling law for active dispersal distance:

$$\alpha_k^{-1} = \alpha_0^{-1} \left(\frac{M_k}{M_0} \right)^d, \quad (19)$$

where their observational data show that $d \approx 0.65$ for mammals. Peters (1983) proposes a similar scaling law for migration distance on the basis of a mixture of submodels for active dispersal and empirical evidence; he finds different values of d depending on the taxon and mode of movement (running, flying, swimming).

In summary, the allometric scaling laws (15), (16), (17), and (19) characterize the body size dependence of each guild k , thus forming the connection between guilds, and contain three shape parameters ($b = a - \hat{a}$, c , and d) and five reference parameters (M_0 , $J_{M,0}$, ν_0 , J_0 , and α_0). The

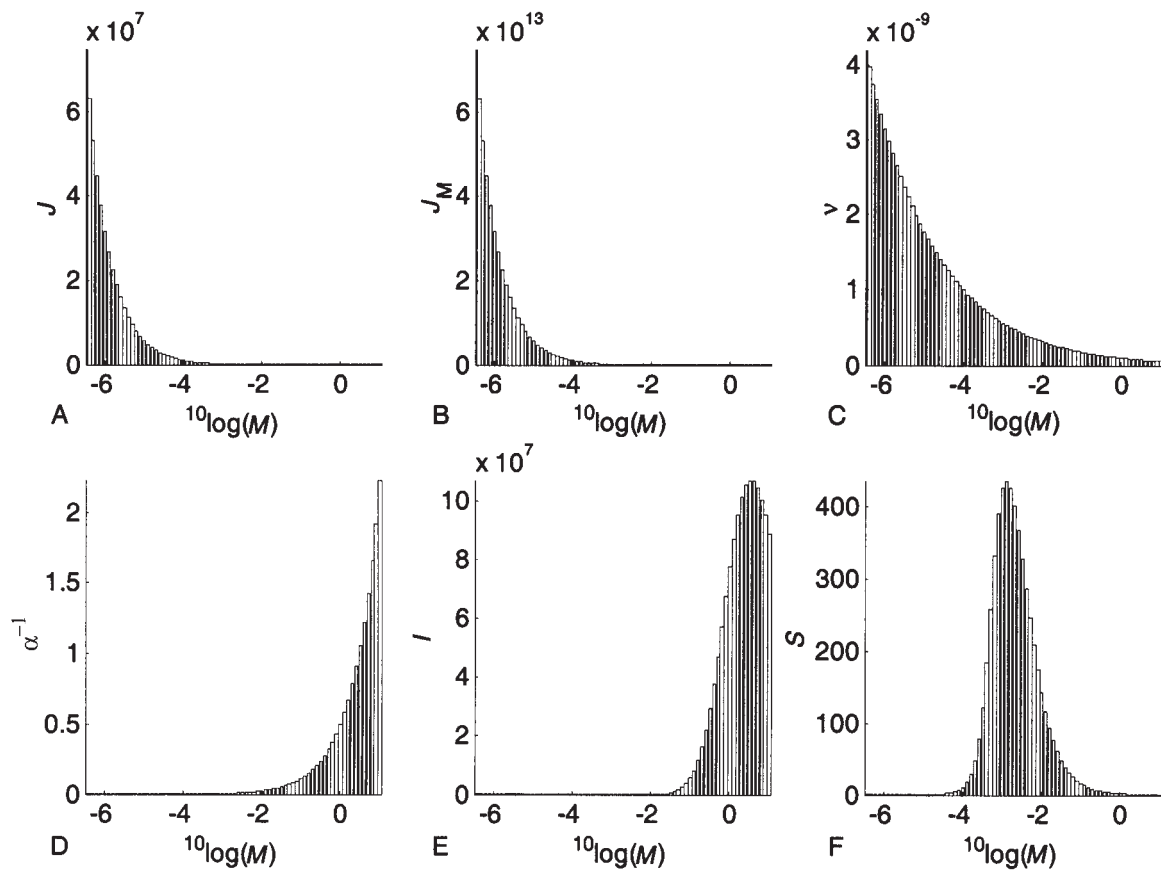


Figure 1: Input and output of our model. Input: allometric scaling laws for the number of individuals in the local community J , the number of individuals in the regional species pool J_M , the speciation rate ν , and the dispersal distance α^{-1} for the default parameter set ($b = -3/4$, $c = -1/4$, $d = 0.65$, $x = 5$, $D = 1$, $r = 0.1$). Output: body size distributions for the number of potential immigrants I and the number of species S (see table 1 for formulas).

reference parameters are unimportant if one is only interested in relative differences between guilds. See also table 1.

Results

We can now insert the allometric relationships (15), (16), (17), and (19) into the within-guild model defined by equations (5) and (7) with either equations (8) or (9) to obtain the dependence of species richness on body mass for the local community. See also table 1 for a summary of the entire model. Values for the parameters must obviously be chosen to draw pictures. The default parameter values are listed in table 1. For the reference parameters (M_0 , $J_{M,0}$, ν_0 , J_0 , and α_0), we chose biologically reasonable values, but the exact values are unimportant, as stated previously. For the allometric scaling parameters (b , c , d), we chose the most commonly reported values, and for the

remaining parameters (x , D , r), we chose relatively arbitrary values, but we studied the sensitivity of the model to these parameters. For this default parameter set, the allometric scaling laws and the resulting body size distributions for the number of immigrants I and the number of species S are shown in figure 1. Note that the optimum for S occurs at a lower body size than the optimum for I . The reason is that the number of species depends not only on I but also on $\theta = 2J_M\nu$, which is a rapidly decreasing function of body size M .

Let us first examine the role of niche width r . Figure 2 shows the species–body size distribution for increasing values of niche width (and therefore decreasing number of niches). At first glance, this looks just like plots of the same distribution with different class widths. But at closer look, we see that the total number of species drops when r increases. This happens because we assumed that the reference guild (with body mass M_0) contains a fixed num-

ber of individuals regardless of r . This is consistent with our definition of a guild as containing functionally equivalent species sharing the same number of resources. The total number of species in the local community therefore relies heavily on niche width.

We varied one parameter at a time to analyze the sensitivity of the model to the three allometric scaling parameters, ignoring the fact that they are not completely independent because they are all related to the allometry of metabolic rate. Figure 3 summarizes the dependence on these parameters. Changes in b and c appear to affect only the scale on the Y-axis and cause a small shift on the X-axis, but the shape of the distribution remains virtually the same. A change in d , however, causes a larger shift on the X-axis and a change in skewness. Because the parameters a and \hat{a} together constitute the composite parameter b , the dependence on either of them can be derived from figure 3 as well: smaller (i.e., more negative) b represents both smaller a when \hat{a} is kept fixed and larger \hat{a} when a is kept fixed.

If d has such a profound effect, a remarkable effect may also be expected from a change in x . Figure 4 confirms this: as x increases, the mode shifts to the right, and the shape changes from left-skewed via lognormal to right-skewed. The change in shape occurs mainly on the left side of the mode. This can be easily understood because on the right side of the mode, there is practically no dispersal limitation. The total number of species also drops considerably with increasing x as could be expected, because larger x makes the dispersal limitation more pronounced. If the model is an appropriate representation of reality, the species–body size distributions found empirically suggest that x is larger than 3 but not so large that it is virtually equal to infinity, indicating that the tail of the dispersal kernel is fatter than assumed in many models.

Finally, we studied how geographic isolation affects the species–body size distribution by changing D , the effective distance between the local community and the regional species pool; isolation increases when D increases. Figure 5 shows the result. The species–body size distribution shifts to larger body sizes as can be expected, because only large species are able to bridge the distance D that separates the local community from the regional species pool. Because the same area can sustain fewer large species, the total number of species also decreases with D .

Discussion

The key proposition in this article is that species that are more similar in size are more functionally equivalent. When species become more functionally equivalent, neutral arguments are expected to gain importance over niche arguments in explaining co-occurrence of species.

In the model that we constructed on this proposition, we assumed that functional similarity is a discrete quantity by dividing all species into functionally different guilds, each consisting of functionally equivalent species. Body size is the key determinant of functional differences, so each guild has its own characteristic body size. The properties of the species in the size guilds (e.g., dispersal distance) are related to an arbitrary reference guild (and hence to one another) by allometric scaling relationships that are power functions of body size, derived using mechanistic considerations or using regression of empirical data. With this framework, we were able to explain the unimodal species–body size pattern for a local community. The crucial element in this explanation is the allometric scaling law of dispersal to body size, and therefore we concluded that dispersal limitation shapes the species–body size distribution.

Our model can also explain multimodal species–body size distributions, such as the bimodal distribution found by Gaston et al. (2001), who report different optima for vertebrates and invertebrates. So far, we assumed that all guilds could be related to a single reference guild by universal allometric scaling laws. Yet taxa differing widely in, for example, type of resources or mode of movement may have different reference parameters. This results in different unimodal distributions that together form a multimodal distribution. Thus, there are several “metaguilds,” each consisting of all size guilds that can be related to one another by a single allometric scaling law.

This division of a metaguild into several size guilds is reminiscent of the division of a resource class into several resource dimensions (De Kroon and Olff 1995). The guild was originally defined as a group of species that exploit the same class of environmental resource in a similar way (Root 1967). Within such a resource class, several resource dimensions can be identified (Platt and Weiss 1977). Our metaguild then corresponds to the guild as originally defined with its associated resource class, and the size guilds correspond to the resource dimensions (but note that different metaguilds may also be distinguished on the basis of other properties than the resource class, such as the mode of movement or metabolism). For example, canopy tree species in a tropical rain forest form a metaguild that has tree-fall gaps as its resource class; resource dimensions are the continuum of the intensity and spectral composition in the gap (Hubbell and Foster 1987). Accepting height as a proxy for body size, trees of similar height belong to the same size guild utilizing the same resource dimension. Species of smaller height may still grow at lower light intensity, thus occupying a different niche, and hence form a different size guild. The significance of the difference in light requirements determines the niche width and thereby whether all trees can be considered as

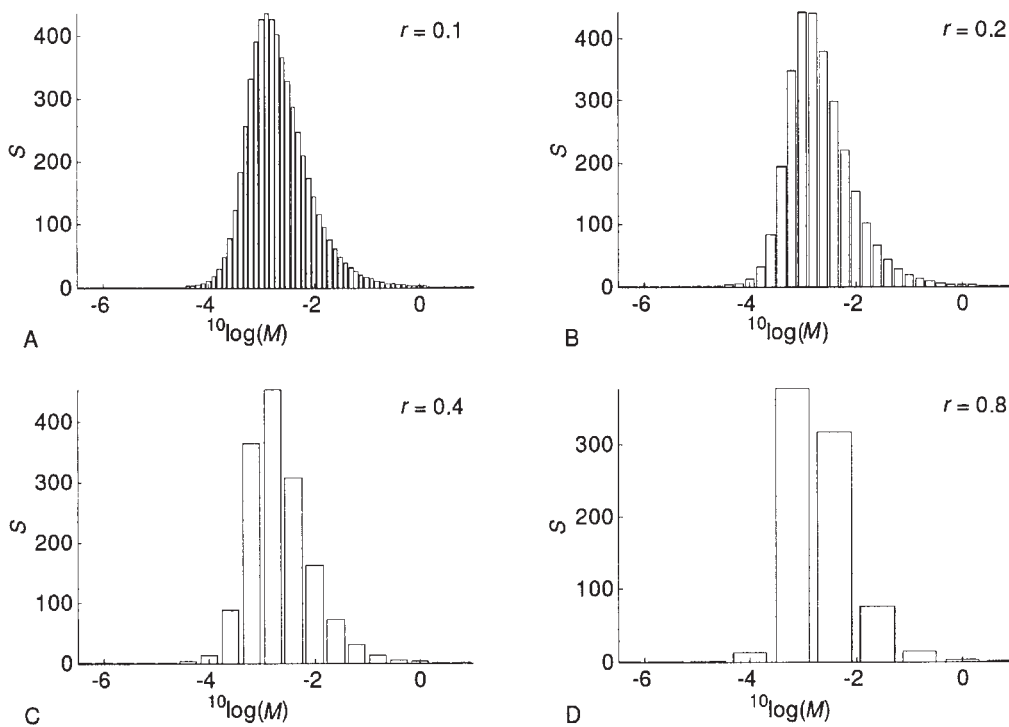


Figure 2: Species–body size distributions for increasing values of niche width r . All other parameter values are from the default parameter set ($b = -3/4$, $c = -1/4$, $d = 0.65$, $x = 5$, $D = 1$).

functionally equivalent or not. Hubbell (2001) argues strongly for functional equivalence in this case. As for a faunal example, grazers in a tropical savanna form a meta-guild with grasses as their resource class. Grass height and grass leaf/stem ratio (a proxy for quality) constitute important resource dimensions. Grazers of larger size tolerate grass of lower quality but require taller grass, thereby creating a separate niche (Olff et al. 2001). Theory that merges such functional differences with neutral processes may explain both the large size range of herbivores in such systems and the co-occurrence of species with the same size (Prins and Olff 1998).

With our model, we also predicted that increasing isolation will lead to a shift of the distribution to larger body size classes. This may seem to be in contradiction with observations, for example, of the absence of large mammals on islands, but one must check whether the assumptions of our model are satisfied. In this example, the essential condition that larger animals have larger dispersal distances is not met. Therefore, we maintain that our prediction merits further study.

For an explanation of a general observed pattern to be acceptable, it must meet (at least) two conditions: the explanation should not depend too critically on specific

relationships or parameter values, since these may be uncertain or vary in time and space (the robustness condition), but at the same time it must be sufficiently sensitive to be able to explain minor deviations from the general pattern (the flexibility condition). We have already shown that different parameter values are able to explain variations in the general pattern, and thus our model seems to meet the condition of flexibility. As regards the robustness condition, we made some simplifying assumptions in our model to make our exposition as transparent as possible, but we now need to scrutinize these assumptions and discuss the possible consequences of relaxation of these assumptions.

We assumed Hubbell's (2001) neutral theory to hold within each guild. Although considerable doubt has been cast on the validity of this theory for entire communities (Abrams 2001; Enquist et al. 2002; McGill 2003), the theory still has a lot of potential for a guild, where we applied it. We do not, however, insist that neutral elements must be part of our explanation of the species–body size distribution. The only crucial element is, as we mentioned above, the behavior of dispersal limitation. A fully niche-based model with a central role for dispersal, for example, the model by Mouquet and Loreau (2002), may also be

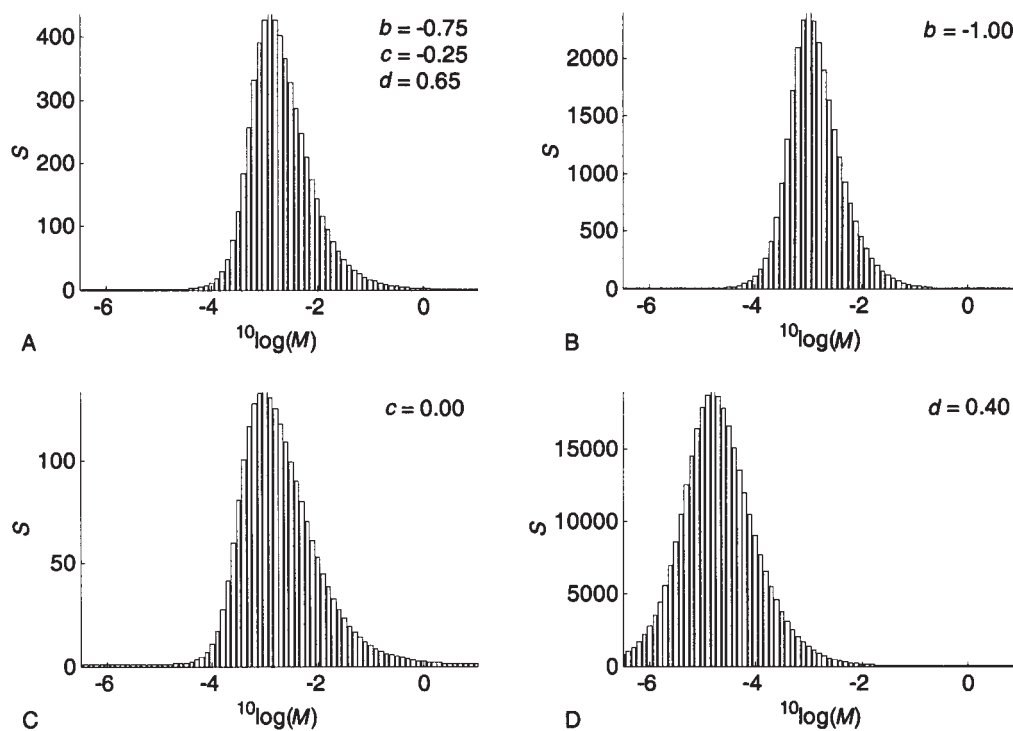


Figure 3: Species–body size distributions for different values of the allometric scaling parameters. The default parameter set is in A, and one parameter is changed in the three remaining panels as indicated. All other parameters have default values ($x = 5$, $D = 1$, $r = 0.1$).

capable of explaining the species–body size distribution. Yet this model is hard to treat analytically, and incorporating body size dependence in it does not seem straightforward, possibly requiring additional assumptions. We believe that our model is very parsimonious using only allometric scaling laws between guilds and neutral processes within guilds.

We have explained the intermediate optimal body size in local communities. However, our model predicts no such optimum in the regional species pool: instead, diversity increases with ever smaller body size. This may seem contradictory. However, the regional species pool may not be adequately described by our model. The model assumes only point mutation and ignores, for example, sympatric speciation by random fission (Hubbell 2001) or allopatric speciation by biogeographic isolation. The rate of speciation in the latter case may depend on active dispersal capacity, hence benefitting large body sizes ($c < 0$ in eq. [17]). This could create an intermediate optimal body size already at the level of the regional species pool. Also, habitat heterogeneity and metacommunity dynamics (including dispersal), which are ignored for the regional species pool, may have a substantial influence (Loreau and Mouquet 1999). Therefore, we do not want to take the contradiction too seriously. Instead, we want to turn the

argument around and state that, even if the regional species pool does not display an intermediate optimal body size, the local community does because of dispersal limitation for small species.

The guilds in our model have no overlap, and the transition from one guild to the next is discontinuous. This may not be fully realistic. Moreover, it contradicts our assumption that species of similar size belong to the same guild in the following way. Species on both sides of the border between two guilds are similar in body size but dissimilar in their properties, whereas species belonging to the same guild but located at the lower and upper borders of the guild share the same properties, although the difference in their body sizes may be much larger. The question is, however, whether our results change qualitatively if continuous transitions are incorporated. Because it is complicated to model this and reduces the transparency of our approach, we refrained from doing so, but we may speculate on what would happen. Species near the border separating two guilds in fact have properties that are averages over both guilds. Hence, we may view these species as constituting a guild of their own. But this is equivalent to decreasing niche width, and figure 2 shows that this has no substantial effect on the qualitative form of the species–body size distribution.

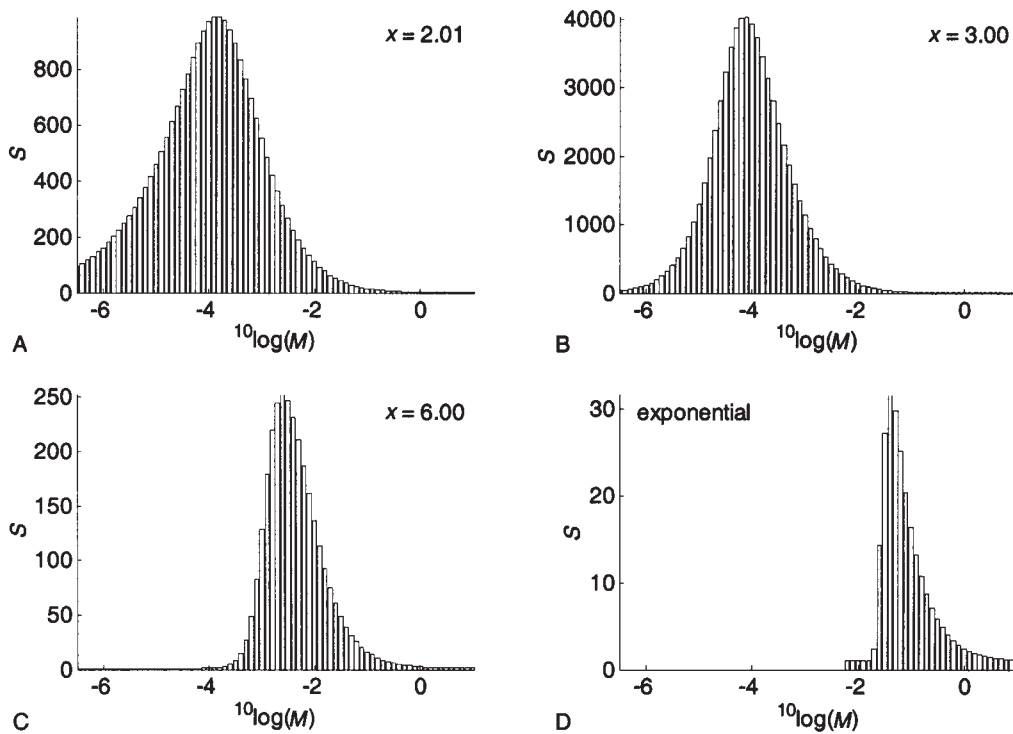


Figure 4: Species–body size distributions for increasing values of the shape parameter x of the dispersal kernel; the dispersal kernel approaches the exponential dispersal kernel as x becomes higher. All other parameters are from the default parameter set ($b = -3/4$, $c = -1/4$, $d = 0.65$, $D = 1$, $r = 0.1$).

In our model, all niches are equally wide in terms of logarithmic body size; that is, $r_k = r$ for all k . In other words, niche width, logarithmically scaled, does not depend on body size, so niche space is scale invariant. This assumption seems intuitively plausible. The logarithmic scale is often the natural scale in ecology because it removes nonlinearities due to exponential growth. Empirical data relating body size to diversity are often presented in logarithmic body size classes of equal length, one of the advantages being that the width of the body size classes is independent of the units in which body size is measured. Still, because these arguments may not be regarded as sufficient reasons, we should consider what might happen if we relaxed this assumption. Minor deviations from $r_k = r$ for all k will result in histograms similar to the figures we presented, only the classes will not be equally wide. For example, if r_k increases weakly with M_k , the bars will be more dense on the left-hand side of the histograms, causing a steeper increase in species number as body size increases followed by a less pronounced decrease when body size exceeds its optimal value. Only if r_k 's dependence on body size is not monotonous and relatively strong, for example, if it first decreases and then increases with body

size, may our (mostly) right-skewed unimodal pattern be lost.

Accepting that $r_k = r$ for all k , we may still be concerned about the correct value of r . Although we stated above that it has no substantial effect on the form of the species–body size distribution (but it does affect the total number of species), one may still wonder whether there is some “natural” class width and how it could be measured. Such a natural class width might be detected from the body size–rank curve. This curve is an alternative way of presenting body size diversity data that does not possess the arbitrariness of class boundaries and displays each data point. Jumps at regular intervals in this curve would suggest that the division into discrete size guilds is warranted, and the interval size would then be an estimate of r .

We assumed that larger species disperse over larger distances—equation (19) with positive d —which likely holds for active dispersal (walking, swimming, flying). If a similar scaling law applies for passive dispersal (transport by wind or water), d would certainly be negative. Hence, if dispersal is predominantly passive, no intermediate optimal body size exists: guilds of smaller body size are always more speciose. Thus, it is crucial to know whether active

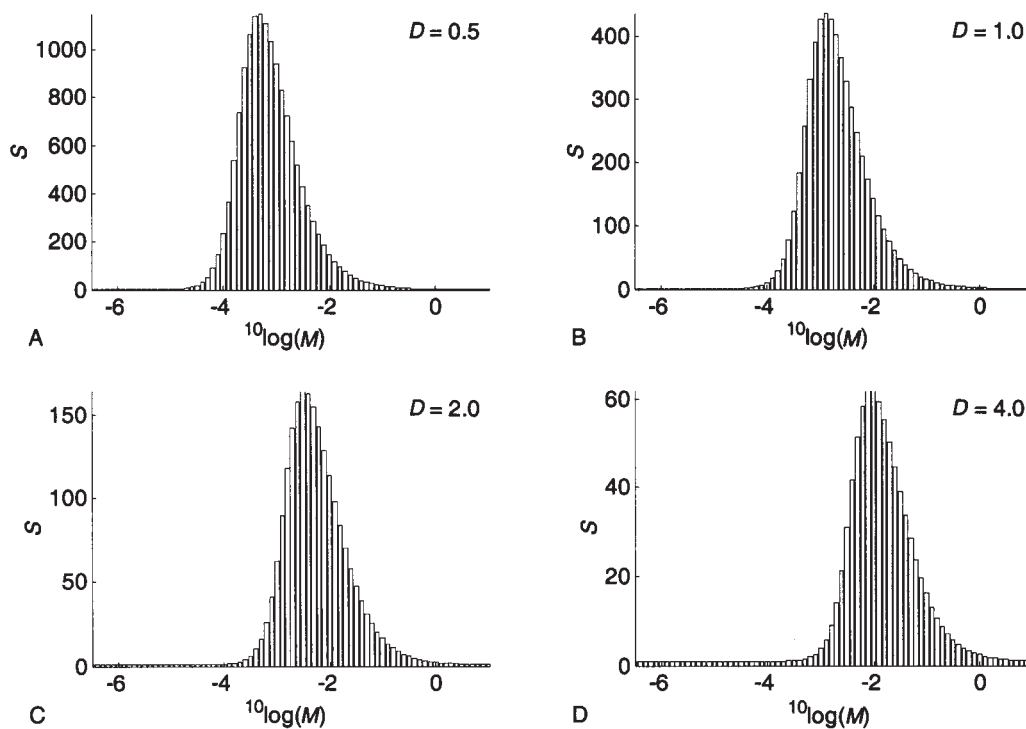


Figure 5: Species–body size distributions for increasing values of D , the effective distance between local community and regional species pool. All other parameters are from the default parameter set ($b = -3/4$, $c = -1/4$, $d = 0.65$, $x = 5$, $r = 0.1$).

or passive dispersal dominates. Unfortunately, examples of species–body size distributions where only passive dispersal is present are hard to find. Passive dispersal is encountered in plants, but for plants the species–body size relationship does not make much sense (since it is the seeds that disperse, not the individuals themselves). In animals, passive dispersal is encountered in insects or fish, but active dispersal is not negligible. Only for very small taxa may predominantly passive dispersal be expected, and, indeed, there are some indications that the classes of smallest body size are most speciose (Azovsky 2002).

Our allometric scaling law for the speciation rate, equation (17), is not (yet) generally accepted and should be tested against more data. However, this relationship is not essential, because even if speciation rate is independent of body size, which is the most likely alternative, the species–body size distribution is still obtained, as shown in the bottom left panel of figure 3, where we set $c = 0$. More generally, if $b + c < 0$, which is satisfied for all realistic parameter values we mentioned, the unimodality and right-skewness is conserved.

Our results depend heavily on the relationship between the number of individuals in a size guild and body size, because J and J_M enter the formulas several times. To our knowledge, there are no data available on this particular

relationship, probably because thinking in terms of size guilds is relatively novel. Data exist, however, on a related pattern, the abundance–body size relationship, but unanimity about its form has not been reached (Gaston and Blackburn 2000). There are many studies indicating a power law with negative exponent with value around -0.75 , but positive values are also found (Blackburn and Gaston 1997), and the explanatory value of body size is often so low that polygonal relationships have been suggested to describe the pattern. The relationship between number of individuals in a size guild and body size can in principle be obtained from abundance–body size data by summing the abundances of all species in the same size guild, but there is no guarantee that all species in a size guild are represented. Given these doubts about extrapolation of these data and the ambiguity about the form of the abundance–body size relationship, we tried a deductive approach by expressing the number of individuals in a size guild in terms of the available resources R_k and body size specific to the resource use \hat{R}_k . The dependence on body size of the latter has been reasonably well established, but not much is known about the former. We assumed a power law (eq. [13]), but this is certainly not undisputed. More data are necessary to confirm or refute this relationship. Even if, for the sake of argument, we

accept it, we can still debate the value of a . The null model is evidently $a = 0$, which means that all species have an equal share of the available resources (or energy); this is called the energetic equivalence rule (Griffiths 1998; Gaston and Blackburn 2000; Allen et al. 2002). The fractal nature of resource perception (Morse et al. 1985) by which small species perceive more resources within the same area than large species suggests that $a < 0$ (a is related to the fractal dimension), and so does the apparent advantage of small species in scramble competition (Gaston and Blackburn 2000). At the same time, superiority of large species in direct interference (contest) competition (Gaston and Blackburn 2000) and handling of low food quality (Ritchie and Olff 1999; Olff et al. 2001) yields $a > 0$. Fortunately, comparison of the top panels of figure 3 shows that our results are not extremely sensitive to $b = a - \hat{a}$, as long as b remains negative. Yet if the relationship differs markedly from equation (13) with negative b , any species–body size distribution may result. For example, if the aforementioned mechanisms play a role in different parts on the body size axis, the relationship for R_k will be U shaped (with the U perhaps upside down), possibly affecting the species–body size distribution significantly.

One of the most plausible alternative mechanisms is that different R_k 's represent different trophic levels: guilds of body size k (and lower) constitute the resources for guilds of body size $k + 1$ (and higher). If this is so, our scaling law for J_k becomes a recurrent relationship. In appendix D in the online edition of the *American Naturalist*, we show for a (speculative) example that this may again result in a simple power law but also in U-shaped relationships that may upset the explanation of the species–body size distribution. But since this is no more than speculation, we believe that it should be interpreted as a warning and a motivation to find the correct scaling law for J_k .

All in all, we believe that our model is fairly robust to relaxation of the assumptions in most instances, and where it is not, it is not clear in what direction assumptions must be relaxed. Hence, our model explains the species–body size pattern well until conclusive evidence to the contrary is found. Moreover, we hope that our approach kindles the debate on the relative importance of niche-based and neutral theories by presenting a model in which elements of both are embedded.

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